Vol. 3 No. 1 page 11-15
DOI: 10.14456/randk.2017.4

RESEARCH & KNOWLEDGE

Research Article

New data on Cretaceous freshwater hybodont sharks from Guangxi Province, South China

Gilles Cuny[1,*], Jinyou Mo[2], Romain Amiot[1], Eric Buffetaut[3,4], Suravech Suteethorn[4], Varavudh Suteethorn[4] and Haiyan Tong[4,5]

[1] Univ Lyon, Université Claude Bernard Lyon 1, ENS de Lyon, CNRS, UMR 5276 LGL-TPE, F-69622, Villeurbanne, France
[2] Natural History Museum of Guangxi, Nanning 530012, China
[3]CNRS (UMR 8538), Laboratoire de Géologie de l'Ecole Normale Supérieure, PSL Research University, 24 rue Lhomond, 75231 Paris Cedex 05, France
[4]Palaeontological Research and Education Centre, Mahasarakham University, Kantarawichai, Mahasarakham 44150, Thailand.
[5]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science Beijing 100044, China

(Received 18 April 2017; accepted 22 May 2017)

Abstract - The Lower Cretaceous Xinlong Formation in Guangxi Zhuang Autonomous region, which was deposited in a non-marine, fluvial environment, has yielded a diverse assemblage of vertebrates. The study of the shark teeth from the Xinlong Formation revealed the presence of teeth of *Acrorhizodus khoratensis* that do not appear to correspond to a jaw position retrieved in Thailand. It also provides a new understanding of the systematic affinities of the species *"Hybodus" aequitridentatus*. The latter does not belong to te genus *Hybodus* but to a new genus belonging to the family Thaiodontidae. The material found in the Xinlong Formation also questions our understanding of the heterodonty pattern of the genus *Acrorhizodus* and highlights how peculiar this genus is among Hybodontiformes. As only two teeth differ significantly from the material retrieved in Thailand, it is difficult to assess whether the Chinese material includes a species different from the Thai one, but it certainly calls for a careful reappraisal of all the available material to better assess the heterodonty pattern of this genus.

Keywords: Hybodont sharks, Cretaceous, Asia, freshwater, endemism

1. Introduction

The Lower Cretaceous Xinlong Formation in Guangxi Zhuang Autonomous region, which was deposited in a non-marine, fluvial environment, has yielded a diverse assemblage of vertebrates including hybodont sharks, actinopterygians (Halecomorphi and Ginglymodi), turtles (the adocid *Shachemys* and the carettochelyid *Kizylkumenys),* crocodilians (cf. *Theriosuchus)* and dinosaurs (the sauropods *Fusuisaurus* and *Liubangosaurus,* carcharodontosaurid and spinosaurid theropods, iguanodontians and a possible psittacosaurid) (Mo *et al*., 2016). The hybodonts encompass five species: *"Hybodus" aequitridentatus, Heteroptychodus steinmanni, Khoratodus foreyi, Acrorhizodus khoratensis* and *Thaiodus ruchae,* the same assemblage being found in the Khok Kruat Formation of Thailand (Cappetta *et al*., 2006; Cuny *et al*., 2008). An Aptian age, similar to that of the Khok Kruat Formation, has therefore being proposed for the Xinlong Formation (Mo *et al*., 2016).

The study of the shark teeth from the Xinlong Formation revealed the presence of teeth of *Acrorhizodus khoratensis* that do not appear to correspond to a jaw position retrieved in Thailand. It also provides a new understanding of the systematic affinities of the species *"H." aequitridentatus*. We shall therefore focus on these two species in the present article.

2. Material and method

The material was surface collected during successive field parties and is housed in the collection of the Natural History Museum of Guangxi (NHMG) in the city of Nanning. It was photographed using a LEICA numerical station equipped with a focus stacking software. The descriptive term 'file' is here used according to Cappetta (2012) and the use of the term 'root' does not imply direct homology with the root of the teeth of other gnathostomes (Underwood *et al*., 2015).

*Author for correspodence: gilles.cuny@univ-lyon1.fr

3. Results

Class: Chondrichthyes Huxley, 1880
Cohort: Euselachii Hay, 1902
Order: Hybodontiformes Patterson, 1966
Family: Thaiodontidae Cuny, Suteethorn, Khamha and Buffetaut, 2008
Genus nov.
"Hybodus" aequitridentatus Cuny, Suteethorn, Khamha and Buffetaut, 2008
Fig. 1F-I

One tooth of *"Hybodus" aequitridentatus* (NHMG 027698), although broken, provides information that leads to a better understanding of the systematic relationships of this species. It measures 5.6 mm mesio-distally, 3 mm labio-lingually and is 2.6 mm high. The root is not preserved. NHMG 027698 displays a low, blunt main cusp ornamented with a dense pattern of anastomosed ridges that do not reach the base of the crown (Fig. 1F, H, I). The lingual face is short and concave in mesial or distal view, whereas the labial one is more developed and almost straight (Fig. 1G). Although an asymmetrical crown with a labial face more developed than the lingual one has been mentioned by Cappetta *et al*. (2006), all the teeth figured so far were anterior ones and this asymmetry was not too marked (Cuny *et al*., 2003, 2008; Cappetta *et al*., 2006), leading to a provisional attribution of this species to the genus *Hybodus* (Cuny *et al*., 2008). On the contrary, the outline of the transverse section of NHMG 027698 is very similar to that of *Thaiodus ruchae* Cappetta *et al*., 2006 and *Khoratodus foreyi* Cuny *et al*., 2008. The genus *Hybodus* is most probably polyphyletic (Cappeta, 2012) and in need of a revision, which has started with the erection of genera such as *Egertonodus* Maisey, 1987, *Meristodonoides* Underwood and Cumbaa, (2010), *Planohybodus* Rees and Underwood, (2008), *Secarodus* Rees and Underwood, (2008) and *Crassodus* Maisch and Matzke, (2016). The presence of a labio-lingually asymmetric crown with a flared labial face was never observed in any tooth attributed to *Hybodus* or to the five above-mentioned genera and such a character remains restricted to the family Thaiodontidae. Therefore, although its ornamentation is more developed than in the two other members of this family, the morphology of the posterior teeth of *"H." aequitridentatus* strongly suggests that this species belongs to the family Thaiodontidae and should be removed from the genus *Hybodus*.

Family *incertae sedis*
Genus: *Acrorhizodus* Cappetta, Buffetaut, Cuny and Suteethorn, 2006
Acrorhizodus khoratensis Cappetta, Buffetaut, Cuny and Suteethorn, 2006
Fig. 1A-E

Most of the teeth of *Acrorhizodus* retrieved from the Xinlong Formation display the same morphology as those of the Thai species *A. khoratensis*: the crown is rectangular in apical view whereas in mesial or distal view the short labial face is convex and the flared lingual face is concave. The ornamentation originates from a U-shaped longitudinal crest and is made of anastomosed ridges reaching the base of the crown. The root, when preserved, shows a labial face inclined lingually and is at least as high as the crown (Fig. 1A-C). One tooth (NHMG 027693) is, however, unusual when looking at the base of the lingual part of the crown, where the ridges are oversized, forming a relief oriented mesio-distally (Fig. 1B-C). It measures 6.5 mm mesio-distally, 7.5 mm labio-lingually and is 12.4 mm high, a size in accordance with the range observed in the Thai material (Cuny *et al*., 2008).

When compared with the material described from Thailand (Cappetta *et al*., 2006; Cuny *et al*., 2008), the main cusp of NHMG 027693 appears a little higher than average. The unusual ornamentation at the base of the lingual face of the crown could therefore be related to a position of the tooth close to the symphysis of the jaw.

Another tooth from the Xinlong Formation (NHMG 033720) also appears unusual. Only the crown is preserved. It is quite flattened and displays a heart-like shape in apical view (Fig. 1D). It shows a U-shaped longitudinal crest with sub-parallel ridges on the lingual face, an ornamentation pattern typical of the genus *Acrorhizodus* but here, the lingual face is less developed than the labial one, a pattern that is actually the reverse of that of *Acrorhizodus* teeth. The tooth measures 2 mm mesio-distally and 2.5 mm labio-lingually, so it is significantly smaller than NHMG 027693. As the crown is much lower than in the latter, it would be tempting to interpret this tooth as a more posterior one than NHMG 027693. However, the teeth interpreted as posterior ones in *A. khoratensis* from Thailand show a different morphology. They are parallelogram-shaped, the longitudinal crest loses its U-shape and the lingual face of the crown is more developed than the labial one (Cuny *et al*., 2008). Clearly, NHMG 033720 does not fit this pattern and its position in the jaws remains difficult to assess. Again, as a single tooth has been retrieved so far, it is difficult to test whether this tooth could correspond to a new taxon, or if it points to some kind of heterodonty in this genus that was not noticed so far. *Acrorhizodus* represents indeed a very peculiar hybodont, the phylogenetic relationships of which are still unclear. Reconstructing its heterodonty pattern remains therefore a challenge. One hypothesis might be related to a dignathic heterodonty, like perhaps the presence of a symphyseal file in only one of the two jaws, which could explain the rarity of this morphotype in the fossil record. The presence of a symphyseal file on only one jaw has been observed in both hybodont (*Asteracanthus ornatissimus)* and neoselachian (*Heterodontus portusjacksoni)* sharks (Pfeil, 2010). Moreover, symphyseal teeth can be significantly smaller than the rest of the teeth forming the dentition (Smith *et al*., 2013). Alternatively, NHMG 033720 could represent a pathological condition.

Finally, one worn tooth (NHMG 033719, Fig. 1E) confirms that the crown of *Acrorhizodus* is made of columnar dentine (Cuny *et al*., 2003), suggesting an adaptation of this genus towards durophagy (Smith and Sansom, 2000).

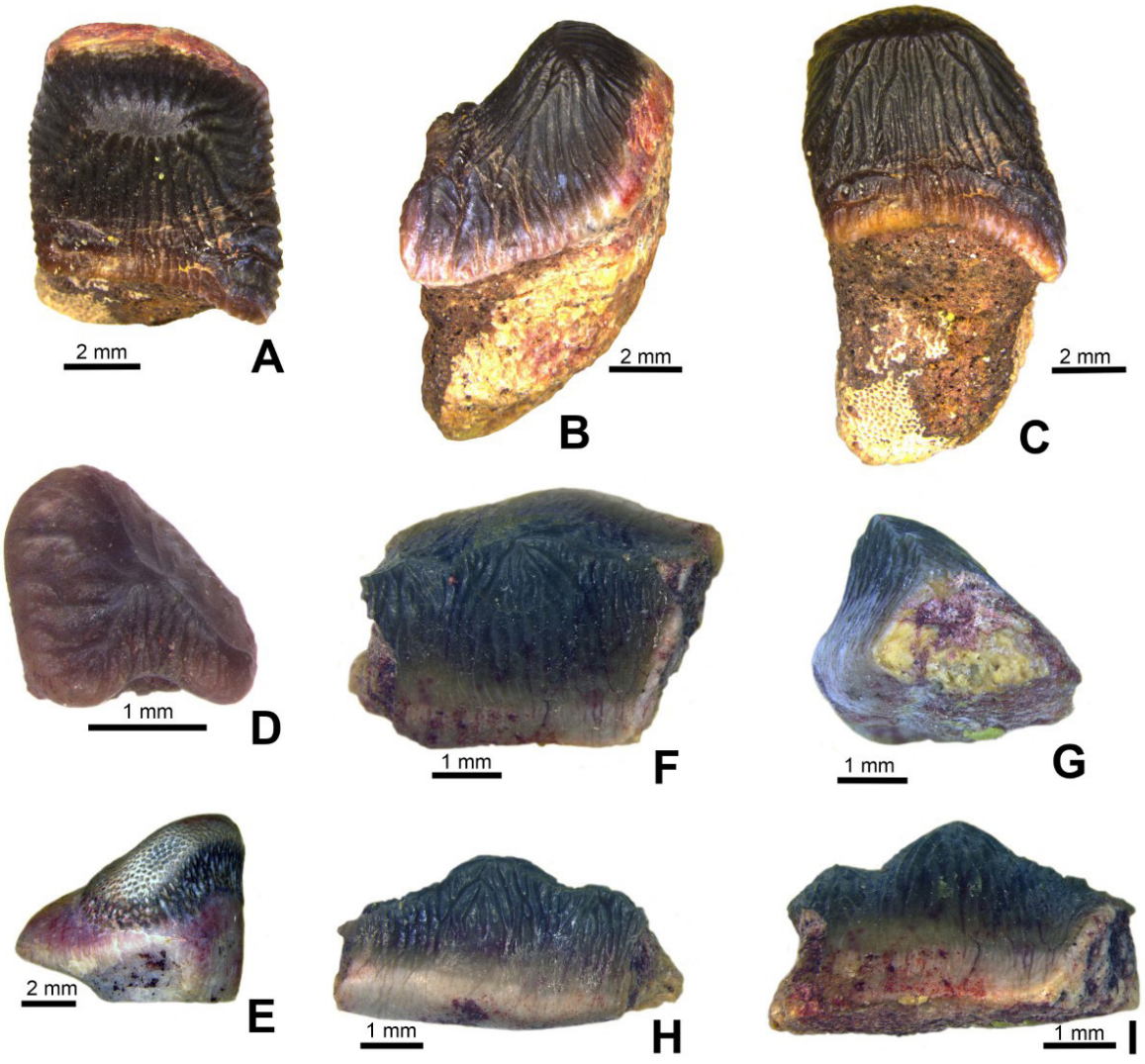

Figure 1. A-E: Teeth of *Acrorhizodus khoratensis*. A-C: Anterior tooth (NHMG 027693) in A, apical, B, distal and C, lingual views. D: Symphyseal (?) tooth (NHMG 033720) in apical view. E: NHMG 033719 in mesial or distal view, the worn crown of which shows the columnar dentine. F-I: *"Hybodus" aequitridentatus* (NHMG 027698) in F, apical, G, mesial or distal, H, lingual and I, labial views.

4. Discussions and conclusions

The material found so far in the Xinlong Formation questions our understanding of the heterodonty pattern of the genus *Acrorhizodus* and highlights how peculiar this genus is among Hybodontiformes. As only two teeth differ significantly from the material retrieved in Thailand, it is difficult to assess whether the Chinese material includes a species different from the Thai one, but it certainly calls for a careful reappraisal of all the available material to better assess the heterodonty pattern of this genus.

The teeth of *"H." aequitridentatus* from the Xinlong Formation demonstrate that this species does not belong to the genus *Hybodus* or to a closely related genus, but to a new genus belonging to the family Thaiodontidae. This reinforces the endemic nature of the freshwater hybodont shark assemblage from Southeast Asia. The five genera currently known from the Aptian of this region are indeed endemic at least at the familial level, and four of them (*Acrorhizodus, "H." aequitridentatus, Thaiodus* and *Khoratodus)* are restricted to the Aptian-Albian interval (Cuny, 2012). The fifth one, *Heteroptychodus,* appeared in the earliest Cretaceous and is restricted to East Asia (Cuny *et al*., 2014; Okazaki, 2016). These five genera cover a wide array of dental specializations: cutting for *Thaiodus,* crushing for the other Thaiodontidae and *Acrorhizodus*, and grinding for *Heteroptychodus*.

The hybodonts from the Khok Kruat and Xinlong formations belong to the *Heteroptychodus-Thaiodus* Province as defined by Cuny (2012) and represent therefore the last stage of a major diversification event of hybodont sharks in freshwater settings. This diversification pattern was, however, a complex one with an important faunal turn-over at the familial level between the Barremian and the Aptian, witnessing the disappearance of specialized genera like *Isanodus* and *Mukdahanodus*. Only the genus *Heteroptychodus* appears to cross this boundary. *Mukdahanodus,* like *Thaiodus,* possessed a highly specialized cutting dentition, a rare feature among hybodont sharks.

So did *Thaiodus* competitively replaced *Mukdahanodus* or was it an opportunistic replacement? If the last hypothesis is true, then it is likely that environmental changes led the "Sao Khua" assemblage (Cuny, 2012) to disappear and freed ecological niches that were mostly invaded by the Thaiodontidae, explaining the rapid diversification of this family. Interestingly, Amiot *et al*. (2009) observed a significant shift in oxygen isotope compositions of *Lepidotes* fish scales between the Sao Khua locality of Phu Phok ($\delta^{18}O$ = 15.4±0.2‰ V-SMOW, N=13) and the Khok Kruat one of Khok Pha Suam ($\delta^{18}O$ = 17.7±0.2‰ V-SMOW, N=16). This ~2‰ shift hints to a significant change in local hydrological or climatic conditions, as previously proposed (Amiot *et al*., 2009), that could have actually been of a larger scale as evidenced by a cold episode recorded in the oxygen isotope compositions of East Asian dinosaurs (Amiot *et al*., 2011) or by a cooling of the Atlantic Ocean during the Late Aptian associated with a biotic crisis (McAnena *et al*., 2013). This cooling trend is possibly at the origin of the observed freshwater fish turn-over. However, the fossil record does not yet allow testing this scenario and tracing the appearance of the first members of the Thaiodontidae. The *Heteroptychodus-Thaiodus* province appears therefore more than ever a formidable laboratory to better understand the mechanisms driving the diversification of hybodont sharks in freshwater environments.

Acknowledgements

We would like to thank Xie Shao-wen, Huang Chao-Lin, Jiang Shan, Lei Xue-Qiang and Xiong Duo for their help in the field. All photographs in (Fig. 1) were taken by Lei Xue-Qiang. Comments from Jürgen Kriwet and an anonymous reviewer greatly enhanced the first version of this manuscript. This work was funded by the CNRS PICS program (grant n°PICS07193) and the Natural Science Foundation of Guangxi (2016GXNSFAA380009)

References

Amiot, R., Buffetaut, E., Lécuyer, C., Fernandez, V., Fourel, F., Martineau, F. and Suteethorn, V. 2009. Oxygen isotope composition of continental vertebrate apatites from Mesozoic formations of Thailand; environmental and ecological significance. In: Buffetaut, E., Cuny, G., Le Loeuff, J. and Suteethorn, V. (Eds.), Late Paleozoic and Mesozoic Continental Ecosystems in SE Asia, Geological Society London Special Publications. The Geological Society, London, pp. 271–283.

Amiot, R., Wang, X., Zhou, Z., Wang, X., Buffetaut, E., Lécuyer, C., Ding, Z., Fluteau, F., Hibino, T., Kusuhashi, N., Mo, J., Suteethorn, V., Wang, Y., Xu, X. and Zhang, F. 2011. Oxygen isotopes of East Asian dinosaurs reveal exceptionally cold Early Cretaceous Climates. Proceedings of the National Academy of Sciences 108, 5179–5183.

Cappetta, H. 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. Verlag Dr. Friedrich Pfeil, München, pp. 512.

Cappetta, H., Buffetaut, E., Cuny, G. and Suteethorn, V. 2006. A new elasmobranch assemblage from the Lower Cretaceous of Thailand. Palaeontology 49(3), 547-555.

Cuny, G. 2012. Freshwater hybodont sharks in Early Cretaceous ecosystems: A review. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiania University Press, Bloomington, pp. 518-529.

Cuny, G., Liard, R., Deesri, U., Liard, T., Khamha, S. and Suteethorn, V. 2014. Shark faunas from the Late Jurassic-Early Cretaceous of northeastern Thailand. Paläontologische Zeitschrift 88, 309-328.

Cuny, G., Suteethorn, V., Buffetaut, E. and Philippe, M. 2003. Hybodont sharks from the Mesozoic Khorat Group of Thailand. Mahasarakham University Journal, 22, special issue, 49-68.

Cuny, G., Suteethorn, V., Kamha, S. and Buffetaut, E. 2008. Hybodont sharks from the Lower Cretaceous Khok Kruat Formation of Thailand, and hybodont diversity during the Early Cretaceous. In: Cavin, L., Longbottom, A. and Richter, M. (Eds.), Fishes and the Break-up of Pangaea. Geological Society, London, Special Publications, 295, 93-107.

Hay, O. P. 1902. Bibliography and catalogue of the fossil vertebrate of North America. Bulletin of the United States Geological Survey 179, 1-868.

Huxley, T. H. 1880. On the application of the Laws of Evolution to the Arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological Society, 1880, 649-662.

Maisch, M. W. and Matzke, A. T. 2016. A new hybodontid shark (Chondrichthyes, Hybodontiformes) from the Lower Jurassic Posidonienschiefer Formation of Dottrenhausen, SW Germany. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 280, 241-257.

Maisey, J. G. 1987. Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. American Museum Novitates 2878, 1-39.

McAnena, A., Flögel, S., Hofmann, P., Herrle, J. O., Griesand, A., Pross, J., Talbot, H. M., Rethemeyer, J., Wallmann, K. and Wagner, T. 2013. Atlantic cooling associated with a marine biotic crisis during the mid-Cretaceous period. Nature Geoscience 6, 558–561.

Mo, J., Buffetaut, E., Tong, H., Amiot, R., Cavin, L., Cuny, G., Suteethorn, V., Suteethorn, S. and Jiang, S. 2016. Early Cretaceous vertebrates from the Xinlong Formation of Guangxi (southern China): a review. Geological Magazine 153(1), 143-159.

Okazaki, Y. 2016. The first report of fossil teeth of *Heteroptychodus* (Hybodontiformes: Elasmobranchii) from the Lower Cretaceous Kanmon Group in Fukuoka Prefercture, northern Kyushu, Japan. Bulletin of the Kitakyushu Museum of Natural History and Human History series A (Natural

History) 14, 1-8.

Patterson, C. 1966. British Wealden sharks. Bulletin of the British Museum (Natural History), Geology 11, 283-350.

Pfeil, F. H. 2010. Ein neues *Asteracanthus*-Gebiss aus den Kieselplattenkalken (Oberjura, Tithonium, Malm Zeta 3, Mörnsheim-Formation) des Besucherstein-bruchs in Mühlheim. Jahresberichte und Mitteilun-gen der Freunde der Bayerischen. Staatssammlung für Paläontologie und Historische Geologie München e.V. 39, 36-60.

Rees, J. and Underwood, C. J. 2008. Hybodont sharks of the English Bathonian and Callovian (Middle Juras-sic). Palaeontology 51, 117-147.

Smith, M. M., Johanson, Z., Underwood, C. and Diekwisch, T. G. H. 2013. Pattern formation in development of chondrichthyan dentitions: a review of an evolutionary model. Historical Biology 25, 127-142.

Smith, M. M. and Sansom, I. J. 2000. Evolutionary origins of dentine in the fossil record of early vertebrates: diversity, development and function. In: Teaford, M. F., Smith, M. M. and Ferguson, W. J. (Eds.), Development, Function and Evolution of Teeth, Cambridge University Press, Cambridge, pp. 65-81.

Underwood, C. J. and Cumbaa, S. L. 2010. Chondrichthy-ans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. Palaeontology 53, 903-944.

Underwood, C. J., Johanson, Z., Welten, M., Metscher, B., Rasch, L. J., Fraser, G. J. and Smith, M. M. 2015. Development and evolution of dentition pattern and tooth order in the skates and rays (Batoidea; Chondrichthyes). PLoS One 10, 1-19.